

A review of the *Eleutherodactylus milesi*-like frogs (Anura, Leptodactylidae) from Honduras with the description of four new species

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Four new species of the *Eleutherodactylus milesi* group are described from the Caribbean versant of Honduras. *Eleutherodactylus stadelmani*, recently resurrected from the synonymy of *E. milesi*, is shown to represent a valid species, but not in the recently suggested concept. A key to the identification of the Honduran members of the *E. milesi* group is also provided.

INTRODUCTION

McCranie et al. (1989) described two new species of streamside frogs of the *Eleutherodactylus milesi* group (*E. chrysozetetes* and *E. cruzi*) from Honduras. These authors also assigned frogs from seven localities across northern Honduras to the species *E. milesi* Schmidt, 1933, although noting that variation occurred among some of these populations in several characters previously used by Savage (1975) to diagnose the species. Campbell (1994) described two new species of this group (*E. adamastus* and *E. trachydermus*) from Guatemala and resurrected *E. stadelmani* Schmidt, 1936 (type locality, Portillo Grande, Departamento de Yoro, Honduras) from the synonymy of *E. milesi*. Campbell (1994) examined two paratypes of *E. stadelmani* (sample 4 of McCranie et al., 1989) and concluded that they were conspecific with a series of frogs from the Quebrada de Oro region, Departamento de Atlántida, Honduras (sample 5 of McCranie et al., 1989) on the one hand, and were distinct from *E. milesi* (sample 6 of McCranie et al., 1989) from the Sierra de Omoa of northwestern Honduras on the other. Campbell (1994) also examined the frogs in samples 2 and 7 of McCranie et al. (1989), but was undecided on the specific identities of these specimens. Unfortunately, the two paratypes of *E. stadelmani* examined by Campbell (1994) are subadults. Had he examined the adults in the type series of *E. stadelmani*, he might have reached different conclusions. Examination by us of the entire type series of *E. stadelmani*, plus a series of frogs recently collected from nearby localities, demonstrates that *E. stadelmani* is indeed a distinct species. Re-examination of the Quebrada de Oro series demonstrates that this population also

represents a species distinct from *E. milesi* (as noted by CAMPBELL, 1994) and *E. stadelmani* as well. In recent years, we have also collected a small series of *E. milesi*-like frogs from forested hillsides well above streams, a previously unknown habitat for frogs of this group. Additionally, a field party from the Museum of Vertebrate Zoology made an incidental collection of *E. milesi*-like frogs while conducting salamander studies in the Sierra de Omoa. Examination of the forest specimens and the MVZ specimens demonstrates that each series also represents an undescribed species (a few additional specimens that are conspecific with the MVZ series were also located in the FMNH and MCZ collections). Finally, re-examination of the series of *E. milesi*-like frogs from the Sierra de Agalta (samples 2 and 3 of McCranie et al., 1989) demonstrated that these specimens represent an undescribed species as well.

Early in this study, when it became apparent that several populations of *E. milesi*-like frogs were morphologically distinct, a decision was made to attempt to collect tissues from as many of these populations as possible. It was hoped that the tissues would substantiate the taxonomic conclusions based on morphological data. Thus, in February 1995, the senior author visited the still pristine Quebrada de Oro-Cerro Búfalo region where three species of the *milesi* group were known to occur (*E. chrysozetetes*, *E. cruzi*, and *E. sp. nov.*). However, in 10 days and nights of collecting, not a single streamside *Eleutherodactylus* was seen, although three species of forest *Eleutherodactylus* were collected well above the nearest streams (the forest *E. milesi*-like frog alluded to above, plus *E. chac* and *E. ridens*). In July 1995, both authors returned to a stream in the Cordillera Nombre de Dios in northern Yoro where *E. stadelmani* was common in July-August of 1991 and 1993. In four daily and nightly visits to this stream by ourselves and/or other members of the field party, no streamside *Eleutherodactylus* were seen, even though there was no change in the streamside vegetation from previous years. *Eleutherodactylus milesi* also was common along small streams that flow into the Rio Cusuco in Parque Nacional El Cusuco, Departamento de Cortés, Honduras, in April 1979, May 1980, August 1982 and July 1983. The senior author searched these same small streams during three days and four nights in August 1992 without seeing a single *E. milesi*. Mario ESPINAL also collected in Parque Nacional El Cusuco on two trips in July-August 1993. Although he collected several specimens of the forest-occurring *E. rostralis* and two species of streamside hylids (*Plectrohyla dasypus* and *P. teuchestes*), no *E. milesi* were collected. These recent collecting efforts suggest that at least some populations of streamside frogs in the *E. milesi* group may be experiencing population declines or have collapsed altogether. Several species of moderate and intermediate elevation streamside frogs have been documented to have disappeared from pristine habitats in Costa Rica and are now feared extinct (K. R. LIPS, J. M. SAVAGE, personal communication). Thus, the possibility exists that one or more of the new species described below may have already vanished from at least their previously known localities.

MATERIALS AND METHODS

Museum abbreviations follow LEVITON et al. (1985): BMNH, Natural History Museum, London, UK; FMNH, Field Museum of Natural History, Chicago, USA; KU, Museum of Natural History, University of Kansas, Lawrence, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; ROM, Royal Ontario Museum, Toronto, Canada; UIMNH, University of Illinois Museum of Natural History, Urbana, USA; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor, USA; USNM, National Museum of Natural History, Washington, USA.

The numbered characters in each species diagnosis follow the standard established by LYNCH & DUELLMAN (1980). Discussion of some of these characters is expanded in the *E. milesi* and *E. stadelmani* sections as no follow up description is provided for either species. Additional to the specimens referred to the four new species described below (see species descriptions), the following Honduran specimens of the *E. milesi* group were examined, which include the holotypes and all extant paratypes of *E. chrysozetetes*, *E. cruzi*, *E. milesi*, and *E. stadelmani*:

Eleutherodactylus chrysozetetes (30). — *Atlántida*: KU 209035 (holotype), 209036; USNM 497054-81.

Eleutherodactylus cruzi (2). — *Atlántida*. KU 209037 (holotype), 209038.

Eleutherodactylus milesi (89). — *Copán*: KU 209076-79, 209097; *Cortés*: FMNH 4699 (holotype), 4700, 4701 (24), 4702, 4704-11, 4713; KU 209040-57, 209060-75, 209107, 209141, LACM 137298-305; MCZ 17435; UIMNH 39946, UMMZ 120388; USNM 118202.

Eleutherodactylus stadelmani (78). — *Olancho*: USNM 497120-68; *Yoro*: FMNH 21862-64; MCZ 21290 (holotype), 21291-92; USNM 497169-91.

We have not recently examined the BMNH specimen of "*E. milesi*" (O'SHEA, 1989, MCCRANIE et al., 1989) reported from the Departamento de Colón, Honduras, and cannot comment upon its specific status. We also follow the lead of CAMPBELL (1994) and do not consider *E. matudai* in this discussion of the *E. milesi* group.

All measurements were made to the nearest 0.1 mm with dial calipers and a dissecting microscope. The following standardized abbreviations for measurements are used (following CAMPBELL, 1994): SVL (snout-vent length), HL (head length tip of snout to angle of jaw), HW (greatest width of head), EL (eye length), E-N (distance between anterior border of eye and posterior border of nostril), TM (tympanum length), E-T (shortest distance between eye and tympanum), TL (tibia length, including covering tissues), FL (distance from posteriormost portion of inner metatarsal tubercle to tip of fourth toe), EW (greatest width of upper eyelid), IOD (shortest interorbital distance), and F3 (disc width of third finger).

Because tympanum condition varies considerably among members of the *milesi* group, we have adopted the following terminology and somewhat subjective criteria: tympanum prominent (annulus distinctly raised and strongly evident throughout its circumference; this condition does not occur in any *milesi* group member); tympanum

distinct (tympanum and annulus covered by thin skin, but annulus evident almost throughout its circumference); tympanum indistinct (tympanum and annulus covered by thicker skin, ca. one-half of annulus evident); tympanum very indistinct (tympanum and annulus covered by thick skin, ca. one-third of annulus evident); tympanum hidden (tympanum and annulus completely concealed by thick skin). The fact that the tympanum may vary from one side of the head to the other in some individuals of those *milesi* group species lacking distinct tympana further compounds the use of this feature. In addition, the tympanum condition is sexually dimorphic. We follow CAMPBELL (1994) in the usage of the terms lateral keels and lateral fringes for the ornamentation of the toes and fingers.

Comparative data for the Guatemalan species *E. adamastus* and *E. trachydermus* are taken from CAMPBELL (1994). Snout shape terminology follows HEYER et al. (1990). Color notes in each diagnosis are taken from preserved specimens. Each diagnosis is based upon adults only, unless otherwise stated.

SYSTEMATIC ACCOUNTS

External characters defining the *E. milesi* group include inner tarsal fold absent, dorsum with scattered to numerous tubercles, tympanum distinct to hidden in males and indistinct to hidden in females, and pale para-anal bars or spots commonly present.

First we provide new diagnoses and distributional statements for *E. milesi* and *E. stadelmani*, followed by the description of four new species of *E. milesi*-like frogs from Honduras. Tables 1-2 compare selected characters among the Honduran members of the *E. milesi* group.

Eleutherodactylus milesi Schmidt, 1933

(fig. 1)

Diagnosis. — (1) Skin of dorsum of head and body, flanks, and upper surfaces of limbs not granular, but wrinkled in most specimens, weakly granular in others; numerous tiny to small tubercles on top of head and anterior part of body; tubercles larger on flanks and posterior part of dorsum of body than on rest of dorsum; margin of upper lip smooth to rough; upper lip not flared; row of raised skin, usually discontinuous, with or without tubercles, forming occipital fold from posterior edge of upper eyelid to scapular region; shorter row of raised skin, with or without tubercles, extending from posterior edge of eye, curving downward above tympanum; skin of venter slightly wrinkled, almost smooth; (2) tympanic annulus distinct in males, indistinct in females, length about 47-68 % length of eye in males, 27-47 % in females; tympanum separated from eye in males by distance 29-47 % length of tympanum, 71-118 % in females; (3) snout nearly rounded to rounded in dorsal view, rounded to nearly vertical (with rounded upper end) in profile; canthus rostralis well defined, angular; loreal region concave; (4) upper eyelid 100-118 % interorbital distance, wrinkled, covered with tiny to large tubercles; no cranial crests; (5) vomerine denticulous processes round to oval in outline, larger than choanae, lateral edge

Tab. 1. - Comparison of selected characters of the Honduran members of the *Eleutherodactylus milesi* group. Abbreviations used are: TM, tympanum length; EL, eye length.

Character	<i>chrysozetetes</i>	<i>cruzi</i>	<i>epochthidius</i>	<i>fecundus</i>	<i>milesi</i>	<i>omoaensis</i>	<i>saltuarius</i>	<i>stadelmani</i>
SVL (mm)								
Males	33.5 - 41.3	27.0 - 33.2	20.9 - 26.9	21.1 - 23.5	19.4 - 25.5	26.2 - 30.0	19.6 - 22.4	27.3 - 33.1
Females	37.3 - 45.6	—	33.1 - 36.7	29.8 - 37.3	25.0 - 37.1	25.6 - 38.4	—	33.2 - 47.4
Male vocal slits	present	present	present	present	present	absent	present	present
Tympanum								
Males	hidden	hidden ¹	indist. to hidden	indist. to hidden	distinct	distinct	dist. to indist.	hidden ¹
Females	hidden	—	indist. to very indist.	indist. to hidden	indistinct	indistinct	very indistinct ²	hidden
TM/EL								
Males	—	—	34 - 39%	36 - 49%	47 - 68%	72 - 85%	35 - 46%	—
Females	—	—	29%	34 - 43%	27 - 47%	39 - 52%	—	—
Upper hp	not flared ³	not flared	not flared	not flared	not flared	flared	not flared	not flared ³
Toe lateral structure	fleshy fringes	fleshy fringes	fleshy fringes	keel ⁴	keel	keel	keel	fleshy fringes

1. Rarely very indistinct

2. In one subadult female, adult females unknown

3. Flared in large females

4. Occasional large females have weakly infolded fringes on toe IV

Tab. 2. - Toe webbing formulae for the Honduran members of the *Eleutherodactylus milesi* group.

Species	Modal webbing formula
<i>Eleutherodactylus chrysozetetes</i>	I 1 1/3 - 2 II 1 1/3 - 2 1/2 III 2 - 3 1/3 IV 3 1/3 - 2 V
<i>Eleutherodactylus cruzi</i>	I 2 - 2 3/4 II 2 - 3 1/2 III 3 [*] - 4 IV 4 - 2 1/2 V
<i>Eleutherodactylus epochthidus</i>	I 2 - 2 3/4 II 2 - 3 1/2 III 3 - 4 1/4 IV 4 1/4 - 2 3/4 V
<i>Eleutherodactylus fecundus</i>	I 2 - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/4 IV 4 1/4 - 2 3/4 V
<i>Eleutherodactylus milesi</i>	I 2 ⁺ - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/2 IV 4 1/2 - 3 [*] V
<i>Eleutherodactylus omoaensis</i>	I 2 - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/2 IV 4 1/4 - 2 3/4 V
<i>Eleutherodactylus salinarius</i>	I - II 2 ⁺ - 3 4/5 III 3 ⁺ - 4 1/2 IV 4 1/2 - 3 [*] V
<i>Eleutherodactylus stadelmani</i>	I 2 - 2 3/4 II 2 - 3 1/2 III 3 [*] - 4 IV 4 - 2 1/2 V

of dentigerous process not extending laterally to median portion of choanae; (6) vocal slits and pale nuptial pads present in males; (7) first finger shorter than second or first and second fingers about equal in length; fingers bearing moderately well developed pads; discs on fingers III-IV slightly broader than long; disc width on finger III 14-36 % length of tympanum in males, 25-56 % in females; (8) fingers bearing lateral keels; (9) no ulnar tubercles on forearm in most specimens, ulnar tubercles on forearm occasionally arranged in linear series, but not developed into fold in those specimens with weakly granular dorsa; antebrachium smooth or with few tiny tubercles; (10) heel varying from nearly smooth with few tiny tubercles to covered with about 30 small tubercles; no linear series of tubercles or fold along outer edge of tarsus; no inner tarsal fold; (11) inner metatarsal tubercle oval to elongate (length about 2-3 times width), 2-3 times size of small rounded outer metatarsal tubercle; no plantar tubercles; (12) toes bearing well developed lateral keel, webbing moderate for *E. milesi* group (modal formula I 2⁺ - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/2 IV 4 1/2 - 3^{*} V); discs on toes III-IV about as broad as or slightly broader than those on fingers III-IV; (13) dorsum of head and body pale brown to dark brown; thin, pale middorsal stripe rarely extending from level posterior to tympanum to vent; larger tubercles with slightly paler colored tips; obscure pale interorbital bar frequently present; dark bars present on upper lip; some individuals with conspicuous pale blotch below canthus; darker crossbars present on dorsal surfaces of limbs; para-anal pale bars or spots well defined, indistinct, or absent; posterior of thigh heavily flecked with brown, with paler brown tiny to small spots or mottling; belly and venter of thigh cream colored, lightly to moderately flecked with brown, belly flecking sometimes coalesced into scattered spots, chin and throat more heavily flecked, especially in some males; (14) adults moderate-sized relative to other members of *E. milesi* group, 25 males 19.4-25.5 ($x = 21.8$) mm SVL, 21 females 25.0-37.1 ($x = 32.1$) mm SVL.

Distribution. - Moderate and intermediate elevations (1050 to 1720 m) of the sierras Omoa and Espiritu Santo of northwestern Honduras (fig. 2). See *Materials and Methods* for a list of specimens examined. The habitat surrounding this species' type locality ("mountains west of San Pedro [Sula], Honduras. Altitude 4500 feet."; SCHMIDT, 1933: 18)

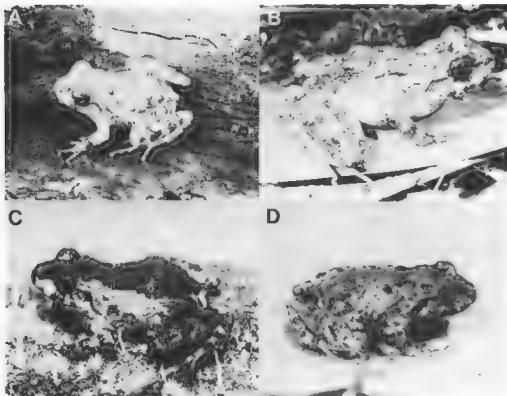


Fig. 1. — (A) Adult male (KU 209049) of *E. miles*, SVL 22.5 mm. (B) Adult female (USNM 497172) of *E. stadelmani*, SVL 46.8 mm. (C) Adult female (USNM 497098) of *E. fecundus*, SVL 33.3 mm. (D) Adult male (USNM 497115) of *E. saltuarius*, SVL 22.4 mm. Photograph (A) by Jim BRIDGES, remainder by senior author.

has been severely altered since SCHMIDT collected the type series. It is unlikely that this species presently occurs at its type locality. Evidence also suggests that the El Cuscu population is experiencing a population decline, or has collapsed altogether (see *Introduction*).

***Eleutherodactylus stadelmani* Schmidt, 1936**

(fig. 1)

Diagnosis. — (1) Skin of dorsum of head and body, flanks, and upper surfaces of limbs not granular to moderately granular, frequently wrinkled, numerous tiny to moderate-sized tubercles on top of head and anterior part of body; tubercles larger on flanks and posterior portion of body than rest of dorsum; margin of upper lip smooth to rough; upper lip usually not flared, sometimes slightly flared in large females; row of raised skin, frequently tuberculate, continuous or discontinuous, forming occipital fold from posterior

edge of upper eyelid to scapular region; shorter row of raised skin, frequently tuberculate, extending from posterior edge of eye, curving downward above tympanum; other short rows of raised skin sometimes present dorsolaterally and on mid-back region; skin of venter usually slightly wrinkled, almost smooth, although moderately wrinkled in some specimens with more granular dorsa; (2) tympanic annulus usually hidden in males (rarely very indistinct), hidden in females; (3) snout nearly rounded to rounded in dorsal view, rounded to nearly vertical (with rounded upper end) in profile; canthus rostralis well defined, angular; loreal region concave; (4) upper eyelid 102-124 % interorbital distance, covered with tiny to large tubercles; no cranial crests; (5) vomerine dentigerous processes round, oval, or somewhat triangular in outline, slightly larger than choanae in males, much larger than choanae in females, lateral edge of dentigerous process not extending laterally to median portion of choanae; (6) vocal slits and pale nuptial pads present in males; (7) first finger shorter than second or first and second fingers about equal in length; fingers bearing moderately well developed pads; discs on fingers III-IV slightly broader than long; (8) fingers bearing lateral keels; (9) no ulnar tubercles on forearm in most specimens, ulnar tubercles on forearm occasionally arranged in linear series, but not developed into fold in those specimens with more granular dorsa; antibrachium smooth with few small to moderate-sized tubercles; (10) heel covered with about 20-40 tiny to moderate-sized tubercles; no linear series of tubercles along outer edge of tarsus; no inner tarsal fold; (11) inner metatarsal tubercle oval to elongate (length about 2-3 times width), 3-5 times size of small rounded outer metatarsal tubercle; no plantar tubercles; (12) toes bearing well developed lateral fleshy fringes that fold ventrally; webbing well developed for *E. milesi* group (modal formula I 2 - 2 3/4 II 2 - 3 1/2 III 3 - 4 IV 4 - 2 1/2 V); discs of toes III-IV about as broad as or slightly broader than those on fingers III-IV; (13) dorsum of head and body pale brown to dark brown, frequently with darker brown mottling or spotting, some specimens with broad, pale dorsolateral longitudinal stripe, others with broad, pale middorsal band beginning on snout and extending laterally to cover upper eyelids and gradually narrowing to V-shape above vent; larger tubercles frequently with slightly paler colored tips; obscure pale interorbital bar frequently present; dark bars present on upper lip; some individuals with conspicuous pale blotch below canthus; darker crossbars present on dorsal surfaces of limbs; para-anal pale bars or spots well defined, indistinct, or absent; posterior of thigh heavily flecked with brown, with paler brown tiny to small spots or mottling; belly and venter of thigh cream colored, lightly to moderately flecked with brown, chin and throat more heavily flecked, especially in some males; occasional specimens have dark flecks on belly, chest, chin, and throat concentrated into mottled or vermiculate pattern; (14) adults large relative to other members of *E. milesi* group, 18 males 27.3-33.1 ($x = 30.2$) mm SVL, 19 females 33.2-47.4 ($x = 39.8$) mm SVL.

Comparisons. — *Eleutherodactylus stadelmani* is easily distinguished from *E. milesi* by its larger size (see above and tab. 1), tympanum condition (hidden or rarely very indistinct in male and hidden in female *stadelmani* versus distinct in male and indistinct in female *milesi*), toe margin structure (well developed lateral fleshy fringes that fold ventrally in *stadelmani* versus lateral keels in *milesi*), and amount of toe webbing (see above and tab. 2). *Eleutherodactylus stadelmani* is apparently most closely related to *E. cruzi* (the latter known only from 1520 m at a single locality in the central portion of the Cordillera Nombre de Dios, Departamento de Atlántida, Honduras), differing from that species only

in color pattern (no pale middorsal stripe in *stadelmani* versus thin, pale middorsal stripe extending from tip of snout to just above vent in *cruzi*) and skin texture (row of raised skin, that is frequently tuberculate, forming well developed occipital fold, numerous tiny to moderate-sized tubercles on heel, and upper eyelid with many tiny to large tubercles in *stadelmani* versus occipital fold indistinct to poorly developed, heel mostly smooth with only tiny tubercles, and much of upper eyelid smooth or wrinkled in *cruzi*). *Eleutherodactylus chrysozetetes* (known only from 880 to 1130 m in the central portion of the Cordillera Nombre de Dios, Departamento de Atlántida, Honduras) is similar to *E. stadelmani* in having well developed fleshy fringes on the toe margins and hidden tympana. However, *E. stadelmani* differs from *E. chrysozetetes* in smaller male size (see tab. 1) and by having less toe webbing (see tab. 2). *Eleutherodactylus stadelmani* is most easily distinguished from *E. adamastus* of Guatemala by tympanum condition (annulus usually hidden, rarely very indistinct in male and hidden in female *stadelmani* versus distinct in male and indistinct in female *adamastus*) and toe margin structure (well developed lateral fleshy fringes in *stadelmani* versus lateral keels in *adamastus*). *Eleutherodactylus stadelmani* can be distinguished from *E. trachydermus* of Guatemala by skin texture (dorsal surfaces not granular to moderately granular and ventral surfaces usually slightly wrinkled, almost smooth in *stadelmani* versus dorsal surfaces strongly granular and ventral surfaces coarsely wrinkled in *trachydermus*), male tympanum condition (annulus usually hidden, rarely very indistinct in *stadelmani* versus indistinct in *trachydermus*) and chin and throat coloration (lightly to heavily flecked with brown in *stadelmani* versus chin and throat with heavy suffusion of dark gray melanophores to almost uniformly brown in *trachydermus*).

Distribution. — Isolated localities at moderate and intermediate elevations (1125 to 1900 m) of northern Honduras from the western portion of the Cordillera Nombre de Dios southward to Montaña de Pijol and eastward to Parque Nacional La Muralla in northwestern Olancho (fig. 2). See *Materials and Methods* for a list of specimens examined. The habitat surrounding this species' type locality ("Portillo Grande, Yoro, Honduras, at 4800 feet altitude"; SCHMIDT, 1936: 44) has been severely altered since the type series was collected and it is unlikely that the species still occurs in the region. Evidence also suggests that the population at the single known locality for the species in the western Cordillera Nombre de Dios may also be declining (see *Introduction*).

Eleutherodactylus omoensis sp. nov.

Holotype — MVZ 115286, adult male, from about 10 airline km WSW San Pedro Sula on road to Perú (15°28'N, 88°06'W), elevation 1150 m, Sierra de Omoa, Departamento de Cortés, Honduras, 9 February 1974, James KEZER and James F. LYNCH.

Paratypes. — Sixteen specimens: MVZ 115283-84, 115287-88 and 115290, all adult males, and MVZ 115281-82, 115285 and 128749-52, all adult females, all with same locality and data as holotype; MCZ 21295-96, both adult males, and FMNH 21820 and 21829, both adult females, all from Montaña Santa Ana W of San Pedro Sula, Departamento de Cortés, Honduras.

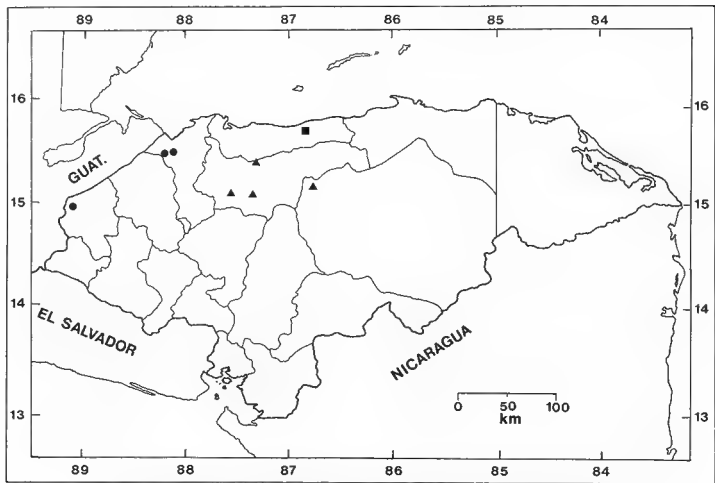


Fig. 2. - Distribution of four species of the *Eleutherodactylus milesi* group in Honduras. Circles: *E. milesi*; triangles: *E. stadelmani*, square: *E. chrysozetetes* and *E. cruzi*. A single symbol may represent more than one locality.

Referred specimens – Seven specimens: MVZ 128754, subadult male, and MVZ 115289 and 128753, both subadult females, same locality and data as holotype; MCZ 21298, subadult male, MCZ 21299, subadult female, and MCZ 21297, juvenile female, all from Montaña Santa Ana W of San Pedro Sula, Departamento de Cortés, Honduras; FMNH 4677, juvenile, from Cañon Santa Ana W of San Pedro Sula, Departamento de Cortés, Honduras.

Diagnosis. – (1) Skin of dorsum varying from not granular, but wrinkled, to strongly granular, with numerous tiny to moderate-sized tubercles, skin of venter slightly wrinkled, almost smooth in many specimens, coarsely wrinkled in those specimens with strongly granular dorsa; (2) tympanic annulus distinct in males, indistinct in females; (3) snout semicircular to nearly rounded in dorsal view, rounded in profile; (4) upper eyelid 100-125 % interorbital distance, usually covered with tiny to large tubercles, rarely wrinkled with relatively few tubercles; no cranial crests; (5) vomerine dentigerous processes oval to nearly triangular in outline; (6) vocal slits absent, pale nuptial pads present in males; (7) first finger shorter than second or first and second fingers about equal in length; fingers bearing moderately well developed pads; (8) fingers bearing lateral keels, (9) ulnar tubercles indistinct; (10) heel bearing small to moderate-sized tubercles; no linear series of tubercles along outer edge of tarsus; no inner tarsal fold; (11) inner metatarsal tubercle elongate, 3-4 times size of small rounded outer metatarsal tubercle; no plantar tubercles; (12) toes bearing well developed lateral keels, webbing moderate (fig. 3) for *E. milesi* group (modal formula I 2 – 2 4/5 II 2 – 3 3/4 III 3 – 4 1/2 IV 4 1/4 – 2 3/4 V); discs of toes III-IV about as broad as or slightly broader than those on fingers III-IV; (13) dorsum of head and body medium brown to dark brown, some specimens with broad, pale dorsolateral longitudinal stripe, others with broad, pale middorsal band beginning on snout and extending laterally to cover upper eyelids and gradually narrowing to V-shape above vent; para-anal pale bars or spots indistinct, occasionally absent, belly and venter of thigh cream colored, lightly to moderately flecked with brown, chin and throat more heavily flecked, especially in some males; (14) adult males large and adult females moderate-sized relative to other members of *E. milesi* group, 8 males 26.2-30.0 ($x = 28.1$) mm SVL, 9 females 25.6-38.4 ($x = 32.2$) mm SVL.

Comparisons. – *Eleutherodactylus omoaensis* is apparently most closely related to *E. milesi* (the latter also known from the Sierra de Omoa). These two species have similar tympanum conditions, toe webbing, and toe margin structure. *Eleutherodactylus omoaensis* differs from *E. milesi* by having flared upper lips (not flared in *milesi*), broader heads (HW 44-48 % of SVL in male and 43-49 % in female *omoaensis* versus 39-43 % in male and 39-42 % in female *milesi*), adult males lacking vocal slits (present in *milesi*), larger adult male size (see above and tab. 1), and larger tympanum size in adult males (see tab. 1). *Eleutherodactylus omoaensis* can be distinguished from all other members of the *E. milesi* group by the following combination of characters: relatively large adult male size and moderate adult female size; tympanic annulus distinct in males and indistinct in females; males lacking vocal slits; moderate toe webbing; and lateral keels on toes.

Measurements of holotype (mm). – SVL 30.0; HL 13.6, HW 14.0; EL 4.0, E-N 3.0, TM 3.4; E-T 1.2; TL 15.5; FL 15.0; EW 3.7; IOD 3.4; F3 0.6.

Colors of holotype in preservative. – Dorsum of head and body dark brown, most of larger tubercles with pale gray tips, dark crossbars on limbs not well marked; iris gray; pale inter-

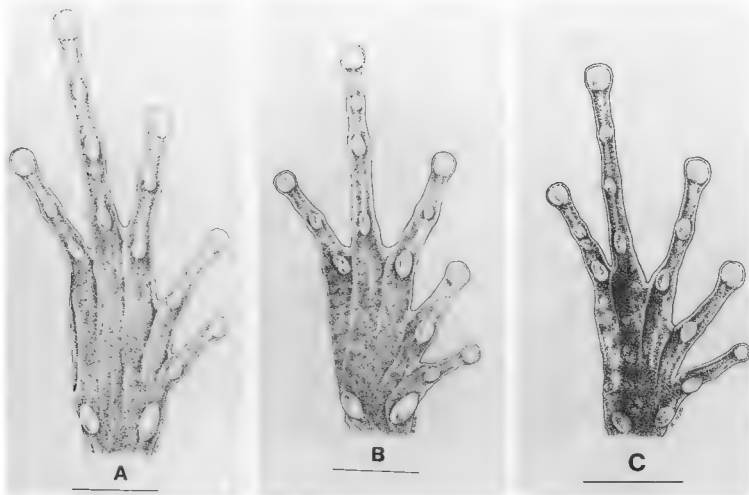


Fig 3. — Ventral view of right foot of (A) *E. omoensis* (MVZ 115282), (B) *E. fecundus* (USNM 497099) and (C) *E. saltarius* (USNM 497115). Each scale bar equals 5 mm. The foot structure of *E. epochthidus* resembles that of *E. fecundus* except that fleshy fringes are present on toes III-IV or toe IV.

orbital bar absent; dark bars on upper lip very obscure; posterior of thigh heavily flecked with brown, with small, pale brown spots, para-anal pale bar indistinct; belly and venter of thigh cream colored, lightly to moderately flecked with brown, chin, throat, and chest more heavily flecked; palmar and plantar surfaces brown with tiny, scattered pale spots.

Description. – The following measurements and proportions are based on the entire type series of eight males and nine females. Head usually wider than long (width 98-109 % of length); HW 43-49 % of SVL; HL 43-46 % of SVL in males, 41-47 % in females; snout semicircular to nearly rounded in dorsal view, rounded in profile, E-N 9-11 % of SVL; upper eyelid usually covered with tiny to large tubercles, upper eyelid rarely wrinkled with relatively few tubercles, EW 100-125 % of IOD. Top of head flat in interorbital region, skin varying from not granular, but wrinkled to strongly granular, with numerous tiny, or numerous tiny plus a few to many moderate-sized tubercles; no cranial crests; canthus rostralis angular; loreal region concave; margin of upper lip smooth to rough; upper lip distinctly flared below and posterior to orbit in both sexes; internarial area slightly concave; nostrils slitlike, protuberant, directed posterolaterally. Supratympanic fold well developed, usually consisting of series of enlarged tubercles on raised skin, extending from posterior edge of eye, but not reaching insertion of forelimb; row of raised skin, usually tuberculate, forming usually discontinuous occipital fold from posterior edge of upper eyelid to scapular region, although fold may be poorly defined in some specimens; shorter row of raised skin, usually tuberculate, extending from posterior edge of eye, curving downward above tympanum; tympanic annulus distinct and rounded in males, evident almost throughout circumference; tympanic annulus indistinct in females, usually evident anteriorly and ventrally; tympanum length about 72-85 % length of eye in males, 39-52 % in females; tympanum separated from eye by distance 26-37 % of tympanum length in males, 70-106 % in females. Choanae smaller than vomerine dentigerous processes, round, teardrop-shaped, or oval in outline, anterior edge flat and formed by anterior lateral process of vomer, not concealed by palatal shelf of maxillary arch; vomerine dentigerous processes about as long as wide, or longer than wide, oval to nearly triangular in outline; vomerine dentigerous processes posteromedial to choanae, lateral edge of dentigerous process not extending laterally to median portion of choanae; vomerine dentigerous processes separated by distance less than width of each dentigerous process, each dentigerous process bearing three to four teeth along posterior border in males, three to six teeth in females. Tongue moderate in size, longer than wide, not notched posteriorly, free posteriorly for about 25 % of its length.

Skin on dorsum of anterior part of body and limbs varying from wrinkled and not granular to strongly granular, skin with numerous tiny or numerous tiny plus a few to many moderate-sized tubercles, skin on posterior part of dorsum and on flanks with larger tubercles; skin of venter slightly wrinkled, almost smooth in many specimens, coarsely wrinkled in those specimens with strongly granular dorsa; skin below vent tuberculate; irregular series of ulnar tubercles or ulnar tubercles sometimes arranged in linear series, but not developed into fold in those specimens with strongly granular dorsa; antibrachium with numerous tiny to small tubercles; heel covered with about 20-30 small to moderate-sized tubercles; no linear series of tubercles or fold along outer edge of tarsus. Cloacal opening directed posteroventrally, slightly below upper level of thigh.

Forearm moderately slender in both sexes; fingers relatively long and slender, thumb about equal to or shorter than second finger; fingers with lateral keels, fingers bearing weakly dilated discs (finger III disc 1.4-2.0 times width of phalanx just proximal to disc), all discs bearing pads, pads about as wide as long; discs on fingers III-IV as broad as or slightly broader than long; disc width on finger III 16-31 % length of tympanum in males, 26-53 % in females; discs of fingers I-II ovoid apically, those of fingers III-IV rounded; relative length of fingers in decreasing order III, IV, II, I or III, IV, II \approx I; subarticular tubercles on fingers rounded to slightly elongate in ventral view, scarcely protuberant, flat to rounded in lateral view; supernumerary tubercles on fingers absent; palmar tubercle cordiform, about as large as or slightly larger than suboval thenar tubercle (thenar tubercle less than twice as long as wide); several small accessory palmar tubercles frequently present, males with pale nuptial pads, but without vocal slits. Hindlimbs short; heels not in contact or barely overlapping when hindlimbs flexed at right angles to axis of body, TL 52-62 % of SVL; FL 50-57 % of SVL. Inner tarsal fold absent; two metatarsal tubercles, inner about three times as long as wide, 3-4 times size of small rounded outer tubercle; no supernumerary tubercles on toes; no plantar tubercles; toes with discs and pads, disc tips broadly rounded; toes bearing well developed lateral keels and moderate webbing, webbing formula I 2 - (2 3/4 - 2 4/5) II (2 - 2⁺) - (3 1/2 - 3 4/5) III (3 - 3⁺) - (4⁺ - 4 1/2) IV (4 1/4 - 4 3/4) - (2 3/4 - 3⁺) V; disc on toe III about as broad as or slightly broader than discs on fingers III-IV; subarticular tubercles on toes slightly longer than wide, somewhat protuberant.

The color in preservative of the entire series essentially agrees with that of the holotype. Some paratypes have a broad, pale middorsal longitudinal band; some have a broad, pale dorsolateral longitudinal stripe on each side; an obscure pale interorbital bar is frequently present; some specimens have a conspicuous pale blotch below the canthus. One subadult male (MVZ 128754) has a thin, pale middorsal stripe extending from the snout to just above the vent.

Etymology. - The name *omoaensis* refers to the Sierra de Omoa, the mountain range where the species occurs.

Distribution and natural history notes. - Moderate elevations (760 to 1150 m) in the Sierra de Omoa W of San Pedro Sula, Honduras (fig. 4). The MVZ specimens of *E. omoaensis* were collected at 1150 m during the day (9 February 1974) from around a small stream flowing through a cafetal (J. F. LYNCH, in litt.). We have not visited this area and can add nothing on the present status of this population. The specimens from Montaña Santa Ana were collected from an unknown elevation in August 1931, whereas the juvenile from Cañon Santa Ana was taken at about 760 m on 21 March 1923. Both of these Santa Ana localities are in an area in which the vegetation has long since been severely altered.

Remark. - The paratypes MVZ 128749-52 of *E. omoaensis* have been ventrally dissected and have their left legs missing.

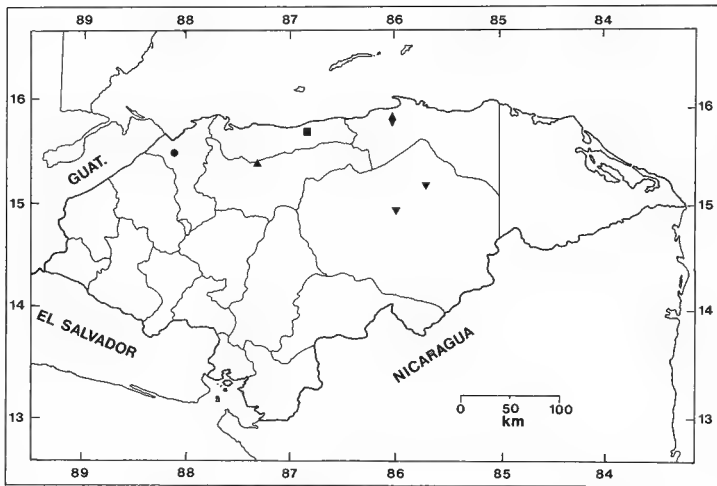


Fig. 4. — Distribution of four species of the *Eleutherodactylus milesi* group in Honduras. Circle *E. omoaensis*; square: *E. fecundus* and *E. saltuarius*; diamond: *E. fecundus*; inverted triangles: *E. epochthidus*; triangle. *E. saltuarius*. A single symbol may represent more than one locality.

***Eleutherodaetylus fecundus* sp. nov.**

(fig. 1)

Holotype. — LACM 137311, adult male, from Quebrada de Oro (15°38'N, 86°47'W), elevation 880 m, tributary of Río Viejo, south slope of Cerro Búfalo S of La Ceiba, Cordillera Nombre de Dios, Departamento de Atlántida, Honduras, 16 August 1982, James R. McCranie, Kenneth L. Williams, and Larry David Wilson. Original number LDW 6322.

Paratypes. — Nineteen specimens: KU 209084-85, 209093, 209099, 209101 and 209142, LACM 137308, USNM 497088 and 497092, all adult males, and USNM 497082-87, 497089-91 and 497093, all adult females, all from the same locality as the holotype, elevation 780 to 1260 m.

Referred specimens. — Fifty-one specimens: KU 209080, 209094, 209143 and USNM 497102, all adult males, KU 209086-92, 209095, 209098, 209100, 209102 and 209104-06, LACM 137306-07 and 137309-10, USNM 497094-96, 497098-101 and 497103-08, all adult females, and KU 206750, 209058, 209081-83, 209096, 209103, 209108 (2) and USNM 497097, all juveniles or subadults, all from the type locality, elevation 780 to 1130 m; MCZ 21293-94, both adult females, from Cordillera Nombre de Dios S of La Ceiba, Departamento de Atlántida, Honduras; USNM 497109, adult female, and USNM 497110-12, all juveniles, from Cerro Calentura, Cordillera Nombre de Dios S of Trujillo, Departamento de Colón, Honduras, elevation 460 m.

Diagnosis. — (1) Skin of dorsum not granular, but wrinkled, with tiny to small tubercles; skin of venter slightly wrinkled, almost smooth; (2) male tympanic annulus indistinct (5 out of 10 specimens in type series), very indistinct (2 out of 10), or hidden (3 out of 10); female tympanic annulus indistinct (4 out of 10 specimens in type series), very indistinct (2 out of 10), or hidden (4 out of 10); (3) snout nearly rounded to rounded in dorsal view, rounded to nearly vertical (with rounded upper end) in profile; (4) upper eyelid 103-133 % interorbital distance, wrinkled, with numerous tiny and about 10-20 small to large tubercles, no cranial crests; (5) vomerine denticerous processes oval or somewhat triangular in outline; (6) vocal slits and pale nuptial pads present in males; (7) first finger shorter than second or first and second fingers about equal in length; fingers bearing moderately well developed pads; (8) fingers bearing lateral keels; (9) ulnar tubercles absent or indistinct; (10) heel bearing small tubercles; no linear series of tubercles along outer edge of tarsus; no inner tarsal fold; (11) inner metatarsal tubercle elongate, 3-4 times size of small rounded outer metatarsal tubercle; no plantar tubercles; (12) toes bearing well developed lateral keel, weakly developed fringes occasionally present on toe IV of large females; webbing moderate (fig. 3) for *milesi* group (modal formula I 2 - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/4 IV 4 1/4 - 2 3/4 V); discs of toes III-IV about as broad as or slightly broader than those on fingers III-IV; (13) dorsum of head and body medium brown to dark brown, some specimens with broad, pale dorsolateral longitudinal stripe on each side, thin, pale middorsal stripe rarely present from level just posterior to eyes to above vent; para-anal pale bars or spots well defined, indistinct, or absent; belly and venter of thigh cream colored, lightly to moderately flecked with brown, chin and throat more heavily flecked, especially in some males; (14) adults moderate-sized relative to other members of

E. milesi group, 10 males 21.1-23.5 ($x = 22.2$) mm SVL, 10 females 29.8-37.3 ($x = 33.5$) mm SVL.

Comparisons. — *Eleutherodactylus fecundus* is most similar to *E. milesi*, but differs in tympanum condition (annulus indistinct, very indistinct, or hidden in male and female *fecundus* versus distinct in male and indistinct in female *milesi*) and amount of webbing on toes III-V (see above and tab. 2). *Eleutherodactylus fecundus* differs from *E. omoaensis* (the apparent closest relative of *E. milesi*) in the same tympanic annulus condition as it does from *E. milesi*. These two species also differ in upper lip condition (not flared in *fecundus* versus flared in *omoaensis*), adult male size (see above and tab. 1), male tympanum size (length about 36-49 % length of eye in *fecundus* versus 72-85 % in *omoaensis*), and male vocal slit condition (present in *fecundus* versus absent in *omoaensis*). *Eleutherodactylus fecundus* can be distinguished from the remaining *E. milesi* group members by the following combination of characters: moderate adult size; indistinct, very indistinct, or hidden tympanic annulus condition in both males and females; moderate toe webbing; and toes with well developed lateral keels.

Measurements of holotype (mm). — SVL 22.1; HL 9.4; HW 9.5; EL 3.2; E-N 1.9; TL 12.9; FL 12.0; EW 2.9, IOD 2.6; F3 0.4.

Colors of holotype in preservative. — Dorsum of head and body medium brown, most larger tubercles with pale gray tips; dark crossbars on limbs well defined; iris gray; pale interorbital bar well defined; dark bars on upper lip well defined; posterior of thigh heavily flecked with brown, with tiny to small pale brown spots; pale para-anal bars fairly well defined; belly and venter of thigh cream colored, moderately flecked with brown, chin and throat more heavily flecked; palmar surface cream colored, moderately flecked with brown; plantar surface cream colored, more heavily flecked with brown than palmar surface.

Description. — The following measurements and proportions are based on the entire type series of 10 adult males and 10 adult females. Head nearly as wide as long to slightly wider than long (width 85-105 % of length); HW 37-46 % of SVL; HL 40-46 % of SVL in males, 38-42 % in females; snout nearly rounded to rounded in dorsal view, rounded to nearly vertical (with rounded upper end) in profile; E-N 7-12 % of SVL; upper eyelid wrinkled with numerous tiny and about 10-20 small to large tubercles, EW 103-133 % of IOD. Top of head flat in interorbital region, skin not granular, but wrinkled, with numerous tiny, or numerous tiny plus scattered small tubercles; no cranial crests; canthus rostralis angular; loreal region concave; margin of upper lip smooth, or smooth with scattered tiny tubercles; upper lip not flared; internarial area slightly concave; nostrils slitlike, protuberant, directed posterolaterally. Supratympanic fold usually well developed, consisting of raised skin, with or without tubercles, extending from posterior edge of eye, but not reaching insertion of forelimb; row of raised skin, with or without tubercles, forming discontinuous occipital fold from posterior edge of upper eyelid to scapular region; shorter row of raised skin, with or without tubercles, extending from posterior edge of eye, curving downward above tympanum; tympanic annulus indistinct (usually evident anteriorly and ventrally), very indistinct (usually evident anteroventrally), or hidden in males and females; tympanum length about 36-49 % length of eye in males ($n = 5$), 34-43 % in females ($n = 4$); tympanum separated from eye by distance 56-67 % of tympanum length in males, 81-85 %

in females. Choanae slightly smaller than vomerine dentigerous processes in males, much smaller than them in females, round, teardrop-shaped, or oval in outline, anterior edge flat and formed by anterior lateral process of vomer, not concealed by palatal shelf of maxillary arch; vomerine dentigerous processes about as long as wide, or longer than wide, oval to nearly triangular in outline; vomerine dentigerous processes posteromedial to choanae, lateral edge of dentigerous process not extending laterally to median portion of choanae; vomerine dentigerous processes separated by distance about equal to or less than width of each dentigerous process; each dentigerous process bearing three to five teeth along posterior border in males, five to eight teeth in females. Tongue moderate in size, longer than wide, not notched posteriorly, free posteriorly for about 25-35 % of its length.

Skin on dorsum of anterior part of body and limbs not granular, but wrinkled, skin with numerous tiny or numerous tiny plus scattered small tubercles; skin on posterior part of dorsum and flanks with larger tubercles; skin of venter slightly wrinkled, almost smooth; skin below vent tuberculate; ulnar tubercles absent, or irregular series of ulnar tubercles present, or ulnar tubercles occasionally arranged in linear series, but not developed into fold; antebrachium smooth or wrinkled, occasionally few small tubercles may be present; heel covered with about 15-30 small tubercles; no linear series of tubercles or fold along outer edge of tarsus. Cloacal opening directed posteroventrally, slightly below upper level of thigh.

Forearm moderately slender in both sexes; fingers relatively long and slender, thumb about equal to or slightly shorter than second finger; fingers with lateral keels; fingers bearing weakly dilated discs (finger III disc 1.3-1.8 times width of phalanx just proximal to disc), all discs bearing pads, pads about as wide as long; discs on fingers III-IV slightly broader than long; disc width on finger III 21-42 % length of tympanum in males ($n = 5$), 31-38 % in females ($n = 4$); discs of fingers I-II ovoid apically, those of fingers III-IV rounded; relative length of fingers in decreasing order III, IV, II, I or III, IV, II \approx I; subarticular tubercles on fingers rounded to slightly elongate in ventral view, scarcely protuberant, flat to rounded in lateral view; supernumerary tubercles on fingers absent; palmar tubercle cordiform or oval, about as large as or slightly larger than suboval thenar tubercle (thenar tubercle less than twice as long as wide); several small accessory palmar tubercles frequently present; males with pale nuptial pads and vocal slits. Hindlimbs short; heels not in contact or barely overlapping when hindlimbs flexed at right angles to axis of body; TL 49-61 % of SVL; FL 44-54 % of SVL. Inner tarsal fold absent; two metatarsal tubercles, inner tubercle about three times as long as wide, 3-4 times size of small rounded outer tubercle; no supernumerary tubercles on toes; no plantar tubercles; toes with discs and pads, disc tips broadly rounded; toes bearing well developed lateral keels (large females occasionally with weakly developed fringes on toe IV) and moderate webbing, webbing formula I (2 - 2⁺) 2 4/5 II 2 (3 1/2 3 4/5) III 3 (4 4 1/2) IV (4⁺ - 4 3/4) - (2 1/2 - 2 4/5) V, disc on toe III about as broad as or slightly broader than discs on fingers III-IV; subarticular tubercles on toes slightly longer than wide, somewhat protuberant.

Color in life of four adult females from the Quebrada de Oro region. - USNM 497095. dorsum dark chocolate brown, broad, irregular ocher dorsolateral stripe extending from posterior of eye to groin; ocher blotch present below canthus; ocher blotch on upper

arm continuous with dorsolateral stripe; dorsum of thigh ocher with brown crossbars; dorsum of tibia banded brown and dark brown; para-anal spots pale orange; chin and chest gray; belly and venter of thigh pale lemon yellow, flecked with brown, iris black with dense gold flecking USNM 497096: dorsum very dark chocolate brown; broad, dark red dorsolateral stripe extending from posterior of eye to groin, dorsal surfaces of limbs very dark chocolate brown; posterior of thigh dark brown; chin and chest dark chocolate brown; belly and venter of thigh lemon yellow, flecked with brown; iris black with dense gold flecking. KU 209100: dorsum dirty dark greenish gray, pale red to rust red spot on rostrum, at forelimb insertion, and on heel; chin and chest gray; belly and venter of thigh lemon yellow with some brown flecking; iris pale copper. USNM 497103: dorsum brown, larger tubercles with slightly darker brown tips; thin, orange middorsal stripe extending from level just posterior to eyes to vent; dorsal surfaces of limbs dark brown; toe and finger discs white dorsally; flanks dark brown; chin and chest pale brown; belly and venter of thigh yellow with brown suffusion.

The color in preservative of the entire series essentially agrees with that of the holotype, except that many specimens have darker brown dorsal surfaces. Some specimens have a broad, pale dorsolateral longitudinal stripe on each side; occasional specimens have a thin, pale middorsal stripe extending from level just posterior to eye to vent; the pale interorbital bar varies from well defined to obscure; some specimens have a pale blotch below the canthus; dark bars are present on the upper lip in most specimens; the pale para-anal bars or spots vary from well developed to indistinct or absent.

Etymology. — The name *fecundus* is Latin, meaning fertile or fruitful. The name is used in reference to the Cordillera Nombre de Dios, the mountain range in which this species occurs, being fertile or fruitful grounds for the discovery of new species of amphibians and reptiles.

Distribution and natural history notes. — Low and moderate elevations (460 to 1260 m) of the Cordillera Nombre de Dios south of La Ceiba and Trujillo (fig. 4), Honduras. The series from the Quebrada de Oro region was collected during May to August alongside streams between 780 to 1260 m in the Premontane Wet Forest formation of HOLDRIDGE (1967). Adults were usually active at night, while juveniles and subadults were active both at night and during the day. No specimens of *E. fecundus* were seen during 10 days and nights of collecting in the Quebrada de Oro region in February 1995 (see *Introduction*), although other Honduran members of the *E. milesi* group (*E. omoaensis*, *E. stadelmani*, and *E. sp. nov.*) have been collected while active during this month. The specimens from near Trujillo were collected in June alongside a stream at 460 m in the Lowland Moist Forest formation of HOLDRIDGE (1967). Data accompanying the MCZ specimens indicate that they were collected in April.

***Eleutherodactylus saltuarius* sp. nov.**

(fig. 1)

Holotype. — USNM 497115, adult male, from south slope of Cerro Búfalo (15°39'N, 86°48'W), elevation 1550 m, Cordillera Nombre de Dios, Departamento de Atlántida,

Honduras, 18 February 1995, James R. McCranie and John C. Rindfleisch. Original number LDW 10432.

Paratypes. — Four specimens: USNM 497117, an adult male, USNM 497119, a subadult male, and USNM 497118, a subadult female, all from 2.5 airline km NNE La Fortuna, Cordillera Nombre de Dios, Departamento de Yoro, Honduras; USNM 497116, a subadult male from the type locality.

Diagnosis. — (1) Skin of dorsum not granular, but wrinkled, with tiny to small tubercles; skin of venter slightly wrinkled, almost smooth; (2) male tympanic annulus distinct or indistinct; tympanic annulus in one subadult female very indistinct; (3) snout nearly rounded in dorsal view, nearly vertical (with rounded upper end) in profile; (4) upper eyelid 100-120 % interorbital distance (including subadult female), wrinkled, with scattered small to moderate-sized tubercles, no cranial crests, (5) vomerine denticerous processes oval to nearly triangular in outline; (6) vocal slits and pale nuptial pads present in males, (7) first finger shorter than second; fingers bearing moderately well developed pads; (8) fingers bearing lateral keels; (9) ulnar tubercles absent; (10) heel mostly smooth or bearing small tubercles; no linear series of tubercles along outer edge of tarsus; no inner tarsal fold; (11) inner metatarsal tubercle oval, 3-4 times size of small rounded outer metatarsal tubercle; no plantar tubercles; (12) toes bearing well developed lateral keel, webbing minimal (fig. 3) for *E. milesi* group (modal formula I - II 2⁺ - 3 4/5 III 3⁺ - 4 1/2 IV 4 1/2 - 3⁺ V); discs of toes III-IV about as broad as those on fingers III-IV; (13) (also includes all subadults) dorsum of head and body dark brown or grayish brown, usually with darker colored spotting on back; para-anal pale bars well defined to indistinct; belly and venter of thigh cream colored, moderately flecked with brown, with some flecking on belly usually coalesced into scattered spots, chin and throat more heavily flecked, becoming uniformly brown in some males; (14) adults small relative to other members of *E. milesi* group, two males 19.6-22.4 ($x = 21.0$) mm SVL, one subadult female 17.8 mm SVL.

Comparisons — Adult males of *E. saltuarius* are somewhat similar in size to those of *E. fecundus* and *E. milesi*. *Eleutherodactylus saltuarius* differs from *E. fecundus* in amount of toe webbing (see above and tab. 2), ventral coloration in preservative (some flecking on belly usually coalesced into spots in *saltuarius* versus belly flecking more or less evenly distributed in *fecundus*) and in life (belly and venter of thigh Clay Color [color 26 in SMITHE, 1975] with numerous spots that were either dark brown or white in *saltuarius* versus yellow with brown flecking in *fecundus*), and habitat (forest floor well away from streams in *saltuarius* versus streamside in *fecundus*). *Eleutherodactylus saltuarius* can be distinguished from *E. milesi* by tympanum condition (annulus distinct or indistinct in male and very indistinct in female *saltuarius* versus distinct in male and indistinct in female *milesi*), male tympanum size (length 35-46 % length of eye in *saltuarius* versus 47-68 % in *milesi*), ventral coloration in life (belly and venter of thigh Clay Color with numerous spots that were either dark brown or white in *saltuarius* versus belly yellow with brown flecking and venter of thigh yellowish orange with brown flecks in *milesi*), and habitat (forest floor well away from streams in *saltuarius* versus streamside in *milesi*). Streamside habitats at the two known localities for *E. saltuarius* are occupied by either *E. cruzi* (Cerro Búfalo) or *E. stadelmani* (NNE of La Fortuna). Both of these species have considerably larger males (to

33.2 mm SVL in *cruzi*, 33.1 in *stadelmani*, 22.4 in *saltuarius*), fleshy toe fringes (lateral keels in *saltuarius*), more toe webbing (see above and tab 2), and usually hidden tympana in males (distinct or indistinct in male *saltuarius*). Juvenile or subadult *E. stadelmani* (USNM 497178: 20.3 mm SVL; USNM 497179: 20.4 mm SVL; USNM 497186: 15.2 mm SVL) from streamside habitats at the La Fortuna locality are easily distinguished from *E. saltuarius* by having well developed toe webbing and fringes. Juvenile or subadult *E. cruzi* are unknown, but presumably have toe fringes and webbing similar to the conditions found in immature *E. stadelmani*.

Measurements of holotype (mm). — SVL 22.4, HL 9.0; HW 8.8, EL 2.9; E-N 2.0; TM 1.0, E-T 0.6; TL 13.7; FL 12.7; EW 2.3; IOD 2.3; F3 0.3.

Colors of holotype in life. — Dorsum Clay Color with larger tubercles on back reddish brown; dorsal and anterior surfaces of limbs Clay Color with darker brown crossbars; posterior of thigh Clay Color with dirty white mottling; belly and venter of thigh Clay Color with numerous spots that were either dark brown or white; chin and throat dark brown; iris pale brown with dark brown reticulations

Colors of holotype in preservative — Dorsum of head and body grayish brown with darker brown spotting on back; darker crossbars on limbs well defined; iris gray; pale interorbital bar indistinct; dark bars on upper lip distinct; posterior of thigh heavily flecked with brown, with cream colored spots and mottling; para-anal pale bars well defined, belly and venter of thigh cream colored, moderately flecked with brown, some flecking on belly coalesced into scattered spots; chin and throat uniformly brown.

Description. — The following measurements and proportions are based on two adult males and one subadult female. Head longer than wide (width 95-98 % of length); HW 39-43 % of SVL; HL 40-41 % of SVL in males, 45 % in subadult female; snout nearly rounded in dorsal view, nearly vertical (with rounded upper end) in profile; E-N 9 % of SVL; upper eyelid wrinkled, with scattered small to moderate-sized tubercles, EW 100-120 % of IOD. Top of head flat in interorbital region, skin not granular, but wrinkled, with numerous tiny, or numerous tiny plus a few small tubercles; no cranial crests; canthus rostrals angular; loreal region concave; margin of upper lip smooth to rough; upper lip not flared; internarial area slightly concave; nostrils slitlike, protuberant, directed posterolaterally. Supratympanic fold not well developed, consisting of raised skin, with or without tubercles, extending from posterior edge of eye, but not reaching insertion of forelimb; row of raised skin, with or without tubercles, forming obscure, discontinuous occipital fold from posterior edge of upper eyelid to scapular region; shorter row of raised skin, with or without tubercles, extending from posterior edge of eyelid, curving downward above tympanum; tympanic annulus distinct and rounded or indistinct (annulus evident anteriorly and ventrally) in males and very indistinct (annulus evident anteriorly) in one subadult female; tympanum length about 35-46 % length of eye in males; tympanum separated from eye by distance 46-60 % of tympanum length in males. Choanae smaller than vomerine dentigerous processes, round, teardrop-shaped, or oval in outline, anterior edge flat and formed by anterior lateral process of vomer, not concealed by palatal shelf of maxillary arch; vomerine dentigerous processes about as long as wide, or longer than wide, oval to nearly triangular in outline; vomerine dentigerous processes posteromedial to choanae, lateral edge of dentigerous process not extending laterally to median portion

of choanae; vomerine dentigerous processes separated by distance less than width of each dentigerous process, each dentigerous process bearing three to four teeth along posterior border in males. Tongue moderate in size, longer than wide, not notched posteriorly, free posteriorly for nearly 50 % of its length.

Skin on dorsum of anterior part of body and limbs not granular, but wrinkled, skin with numerous tiny or numerous tiny plus a few small tubercles; skin on posterior part of dorsum and flanks with a few enlarged tubercles; skin of venter slightly wrinkled, almost smooth; skin below vent tuberculate, no ulnar tubercles, antebrachium smooth, heel mostly smooth or with up to about 10-15 small tubercles; no linear series of tubercles or fold along outer edge of tarsus. Cloacal opening directed posteroventrally, slightly below upper level of thigh.

Forearm moderately slender in both sexes; fingers relatively long and slender, thumb shorter than second finger; fingers with lateral keels; fingers bearing weakly dilated discs (finger III disc 1.5 times width of phalanx just proximal to disc), all discs bearing pads, pads almost as wide as long; discs on fingers III-IV about as broad as long; disc width on finger III 23-30 % length of tympanum in males; discs of fingers I-II ovoid apically, those of fingers III-IV rounded; relative length of fingers in decreasing order III, IV, II, I; subarticular tubercles on fingers rounded to slightly elongate in ventral view, scarcely protuberant, flat to rounded in lateral view, supernumerary tubercles on fingers absent; palmar tubercle cordiform, about as large as oval thenar tubercle (thenar tubercle roughly twice as long as wide), several small accessory palmar tubercles present; males with pale nuptial pads and vocal slits. Hindlimbs short; heels slightly overlapping when hindlimbs flexed at right angles to axis of body; TL 61-64 % of SVL; FL 55-57 % of SVL. Inner tarsal fold absent; two metatarsal tubercles, inner tubercle about two times as long as wide, 3-4 times size of small rounded outer tubercle; no supernumerary tubercles on toes; no plantar tubercles, toes with discs and pads, disc tips broadly rounded, toes bearing well developed lateral keels and minimal webbing, webbing formula I (absent or very basal) II $2^+ - 3 \frac{4}{5}$ III (3 - 3^+) - (4 $\frac{1}{2}$ - 4 $\frac{3}{4}$) IV (4 $\frac{1}{2}$ - 4 $\frac{3}{4}$) - ($3^- - 3$) V; disc on toe III about as broad as discs on fingers III-IV; subarticular tubercles on toes slightly longer than wide, somewhat protuberant.

Color in life of USNM 497116 was recorded as being very similar to that of the holotype. The color in preservative of the paratypes is similar to that of the holotype, except some details: some specimens have dark brown dorsa, the pale interorbital bar is sometimes well defined, a large pale spot occurs posteromedially to the eyes in two specimens, the pale para-anal bars may be indistinct, and one specimen lacks the brown spots on the belly.

Etymology. - The name *saltuarius* is a Latin word meaning "keeper of the sacred forest of Virtue". The name is used in reference to the occurrence of this species in forested habitats well away from streams.

Distribution and natural history notes. - Intermediate elevations (1550 to 1800 m) from two localities in the Lower Montane Wet Forest formation of HOLDRIDGE (1967) in the Cordillera Nombre de Dios of north-central Honduras (fig. 4). Specimens were collected while active during the day on the forest floor in February and August. The forest at both localities for the species was in a primary state with a closed canopy when the specimens

were collected. However, in August 1995, four years after we collected this species NNE of La Fortuna, we found these forests to be in a less than pristine condition. Tracts of forest had been clear cut and burned to make way for crops. Probably not coincidentally, no specimens of *E. saltuarius* were seen at that time, although a concerted effort was made to collect more specimens.

Remarks. — A subadult male *E. saltuarius* (USNM 497116), with a SVL of 14.9 mm, has a single vocal slit on the right side and the nuptial pads beginning to develop.

***Eleutherodactylus epochthidius* sp. nov.**

Holotype. — ROM 18109, adult female, from Río Seco (14°55'N, 85°56'W), elevation 1050 m, tributary of Río Guayape N of Catacamas, Sierra de Agalta, Departamento de Olancho, Honduras, 8 August 1986, James R. MCCRANIE, Kenneth L. WILLIAMS and Larry David WILSON. Original number LDW 8297.

Paratypes. — Ten specimens: ROM 18110 and 18113, both adult males, and ROM 18112, adult female, all from the same locality as the holotype, elevation 1000 to 1060 m; ROM 18100-01 and 18103-05, all adult males, and ROM 18099 and 18102, both adult females, all from between rios Catacamas and Seco, Sierra de Agalta N of Catacamas, Departamento de Olancho, Honduras, elevation 1450 m.

Referred specimens. — Five specimens: ROM 18108, subadult male, and ROM 18111, juvenile, both from the type locality, elevation 1000-1050 m; ROM 18106-07, both juveniles, from between rios Catacamas and Seco, Sierra de Agalta N of Catacamas, Departamento de Olancho, Honduras, elevation 1450 m, KU 209059, subadult female, from Montaña de Malacate ca. 10 airline km NW Dulce Nombre de Culmí, Sierra de Agalta, Departamento de Olancho, Honduras, elevation 760 m.

Diagnosis. — (1) Skin of dorsum not granular, but wrinkled, with tiny to small tubercles; skin of venter slightly wrinkled, almost smooth; (2) male tympanic annulus indistinct (2 out of 7 specimens in type series), very indistinct (4 out of 7), or hidden (1 out of 7); female tympanic annulus indistinct (1 out of 4 specimens in type series) or very indistinct (3 out of 4); (3) snout nearly rounded to rounded in dorsal view, rounded to nearly vertical (with rounded upper end) in profile; (4) upper eyelid 100-121 % interorbital distance, wrinkled, with scattered small to moderate-sized tubercles; no cranial crests; (5) vomerine denticular processes oval or somewhat triangular in outline; (6) vocal slits and pale nuptial pads present in males; (7) first finger shorter than second or first and second fingers about equal in length; fingers bearing moderately well developed pads; (8) fingers bearing lateral keels; (9) ulnar tubercles absent or indistinct; (10) heel bearing small tubercles; no linear series of tubercles along outer edge of tarsus; no inner tarsal fold; (11) inner metatarsal tubercle elongate, 3-4 times size of small rounded outer metatarsal tubercle; no plantar tubercles; (12) toes III-IV or toe IV of males bearing distinct or weak lateral fleshy fringes that fold ventrally, toes III-IV of females bearing distinct lateral fleshy fringes that fold ventrally, remaining toes bearing well developed lateral keels; webbing moderate for *milesi* group (modal formula I 2 - 2 3/4 II 2 - 3 1/2 III 3 - 4 1/4 IV 4

1/4 – 2 3/4 V); disc of toes III-IV about as broad as or slightly broader than those on fingers III-IV; (13) dorsum of head and body pale brown to dark brown, frequently with darker brown blotches or hourglass figure on back; para-anal pale bars or spots well defined, indistinct, or absent; belly and venter of thigh cream colored, heavily flecked with brown; chin, throat, and chest with dense brown flecking surrounding pale "spots"; (14) adults moderate-sized relative to other members of *E. milesi* group, seven males 20.9-26.9 ($x = 24.4$) mm SVL, four females 33.1-36.7 ($x = 35.1$) mm SVL.

Comparisons. – *Eleutherodactylus epochthidius* approaches *E. chrysozetetes*, *E. stadelmani* and *E. cruzi* by having fleshy fringes on toes III-IV (females and some males) or on toe IV only (remaining males) (fleshy fringes present on toes II-IV in *chrysozetetes*, *stadelmani*, and *cruzi*). However, *E. epochthidius* differs from these three species by having less toe webbing (see above and tab. 2), smaller male size (see above and tab. 1), and tympanum condition (usually very indistinct, occasionally indistinct, or rarely hidden versus hidden in *chrysozetetes* and usually hidden or rarely very indistinct in *stadelmani* and *cruzi*) *Eleutherodactylus epochthidius* further differs from *E. cruzi* by lacking a pale middorsal stripe (present in *cruzi*) *Eleutherodactylus epochthidius* is similar to *E. fecundus* in adult size, amount of toe webbing and tympanum condition, but differs from that species by having distinct to rather weak fleshy toe fringes that fold ventrally on toes III-IV (females and some males) or on toe IV only (remaining males), whereas lateral keels are almost always present on toes III-IV in *fecundus* (occasional large females of *fecundus* have weakly infolded fringes on toe IV). *Eleutherodactylus epochthidius* further differs from *E. fecundus* in ventral coloration (usually dense brown flecking on the chin, throat and chest surrounding pale "spots" versus usually moderate flecking that is more or less evenly distributed in *fecundus*) *Eleutherodactylus epochthidius* can be distinguished from the remaining *E. milesi* group members by the following combination of characters: moderate adult size; usually very indistinct, occasionally indistinct, or rarely hidden tympanic annulus condition; moderate toe webbing; toes III-IV or toe IV with distinct to rather weak fleshy fringes; upper lip not flared, and male vocal slits present.

Measurements of holotype (mm). – SVL 35.4; HL 15.3; HW 15.4; EL 5.2; E-N 3.1; TL 22.0; FL 20.5; EW 3.1; IOD 3.1; F3 0.8.

Colors of holotype in life. – Dorsum of body with dark chocolate brown middorsal hourglass figure, rest of dorsum of body brick red; dorsal surfaces of limbs mottled and banded with dark chocolate brown and brick red; chin and throat dark brown with several white spots; chest and anterior portion of belly mottled dark brown and white; posterior portion of belly and ventral surface of thighs pale yellow, rather heavily flecked with brown; palms and soles dark brown; iris dark metallic green.

Colors of holotype in preservative. – Dorsum of head and body pale brown with darker brown hourglass figure on back, most larger tubercles with pale gray tips; dark crossbars on limbs fairly well defined; iris gray; dark bars on upper lip well defined; posterior of thigh heavily flecked with brown, with tiny to small pale brown spots, pale para-anal bars fairly well defined; belly and venter of thigh cream colored, heavily flecked with dark brown; chin, throat, and chest with dense dark brown flecking surrounding pale "spots"; palmar and plantar surfaces densely flecked with dark brown.

Description. — The following measurements and proportions are based on the entire type series of seven adult males and four adult females. Head nearly as wide as long in males (width 95-98 % of length) and slightly wider than long in females (width 101-102 % of length); HW 40-46 % of SVL; HL 41-48 % of SVL; snout nearly rounded to rounded in dorsal view, rounded to nearly vertical (with rounded upper end) in profile; E-N 8-10 % of SVL; upper eyelid wrinkled with numerous tiny and a few small to moderate-sized tubercles, EW 100-121 % of IOD. Top of head flat in interorbital region, skin not granular, but wrinkled, with numerous tiny, or numerous tiny plus scattered small tubercles; no cranial crests; canthus rostralis angular; loreal region concave; margin of upper lip smooth, or smooth with scattered tiny tubercles; upper lip not flared; internarial area slightly concave; nostrils slitlike, protuberant, directed posterolaterally. Supratympanic fold usually well developed, consisting of raised skin, with or without tubercles, extending from posterior edge of eye, but not reaching insertion of forelimb; row of raised skin, with or without tubercles, forming discontinuous occipital fold from posterior edge of upper eyelid to scapular region; tympanic annulus usually very indistinct (annulus usually evident anteroventrally), occasionally indistinct (annulus usually evident anteriorly and ventrally), or rarely hidden; tympanum length about 34-39 % length of eye in males ($n = 2$), 29 % in one female; tympanum separated from eye by distance 79-92 % of tympanum length in two males, 160 % in one female. Choanae slightly smaller than vomerine dentigerous processes in males, much smaller than vomerine dentigerous processes in females, round, teardrop-shaped, or oval in outline, anterior edge flat and formed by anterior lateral process of vomer, not concealed by palatal shelf of maxillary arch; vomerine dentigerous processes about as long as wide, or longer than wide, oval to nearly triangular in outline, vomerine dentigerous processes posteromedial to choanae, lateral edge of dentigerous process not extending laterally to median portion of choanae; vomerine dentigerous processes separated by distance about equal to or less than width of each dentigerous process; each dentigerous process bearing three to four teeth along posterior border in males, five to seven teeth in females. Tongue moderate in size, longer than wide, not notched posteriorly, free posteriorly for about 25-35% of its length.

Skin on dorsum of anterior part of body and limbs not granular, but wrinkled, skin with numerous tiny or numerous tiny plus scattered small tubercles; skin on posterior part of dorsum and flanks with larger tubercles; skin of venter slightly wrinkled, almost smooth; skin below vent tuberculate; ulnar tubercles absent, or irregular series of ulnar tubercles present, or ulnar tubercles occasionally arranged in linear series, but not developed into fold; antibrachium smooth or wrinkled, occasionally with few small tubercles; heel covered with about 10-30 small tubercles; no linear series of tubercles or fold along outer edge of tarsus. Cloacal opening directed posteroventrally, slightly below upper level of thigh.

Forearm moderately slender in both sexes; fingers relatively long and slender, thumb about equal to or slightly shorter than second finger; fingers with lateral keels; fingers bearing weakly dilated discs (finger III disc 1.6-2.0 times width of phalanx just proximal to disc), all discs bearing pads, pads about as wide as long; discs on fingers III-IV slightly broader than long; disc width on finger III 46-57 % length of tympanum in males ($n = 2$), 53 % in one female; discs of fingers I-II ovoid apically, those of fingers III-IV rounded;

relative length of fingers in decreasing order III, IV, II, I or III, IV, II \approx I; subarticular tubercles on fingers rounded to slightly elongate in ventral view, scarcely protuberant, flat to rounded in lateral view; supernumerary tubercles on fingers absent; palmar tubercle cordiform or oval, about as large as or slightly larger than suboval thenar tubercle (thenar tubercle less than twice as long as wide), several small accessory palmar tubercles frequently present; males with pale nuptial pads and vocal slits. Hindlimbs short; heels not in contact or barely overlapping when hindlimbs flexed at right angles to axis of body; TL 54-62 % of SVL; FL 51-58 % of SVL. Inner tarsal fold absent; two metatarsal tubercles, inner tubercle about three times as long as wide, 3-4 times size of small rounded outer tubercle; no supernumerary tubercles on toes; no plantar tubercles; toes with discs and pads, disc tips broadly rounded; toes III-IV or toe IV of males bearing distinct to rather weak lateral fleshy fringes that fold ventrally, toes III-IV of females bearing distinct lateral fleshy fringes that fold ventrally, remaining toes bearing well developed lateral keels; toes with moderate webbing, webbing formula I 2 - (2 1/2 - 2 3/4) II 2 - (3 1/2 - 3 3/4) III 3 - 4 1/4 IV (4⁺ - 4 1/4) - (2⁺ - 2 4/5) V; disc on toe III about as broad as or slightly broader than discs on fingers III-IV; subarticular tubercles on toes slightly longer than wide, somewhat protuberant.

Color in life of an adult female (ROM 18112) was as follows: dorsum of body and head brown with dark outlined pale interorbital bar, bar preceded by and followed by tan blotches; dorsal surfaces of limbs brown with dark brown crossbars; groin golden yellow; chin brown with white punctations; chest mottled brown and white; belly and venter of thigh dirty yellow; palms and soles brown; iris bronze with rust copper band in pupil.

The color in preservative of the type series may be described as follows: dorsum of head and body pale brown to dark brown, frequently with darker brown blotches or hourglass figure on back; pale interorbital bar varying from well defined to obscure; dark bars present on upper lip in most specimens; para-anal pale bars or spots well defined, indistinct, or absent; belly and venter of thigh cream colored, heavily flecked with dark brown, chin, throat, and chest densely flecked with dark brown, flecking surrounding pale "spots" on many specimens, the pale "spots" extending onto belly in occasional specimens. A single subadult female (KU 209059) has much paler ventral surfaces than the remaining specimens, including the other subadult specimen and the juveniles

Etymology - The specific name *epochthidius* is formed from the Greek word *epochthidios*, which means on or of the mountains. The name alludes to the montane habitat of this species.

Distribution and natural history notes. - Moderate elevations (760 to 1450 m) in the Premontane Wet Forest formation of HOLDRIDGE (1967) of the Sierra de Agalta north of Catacamas and northwest of Dulce Nombre de Culmi (fig. 4), Honduras. The series from between the rios Catacamas and Seco was taken in about 30 min of collecting along a small stream just before midday on 5 August 1986. The Río Seco series was collected both during the day and at night along a large stream on 8-9 August 1986. The Montaña de Malacate specimen was collected along a small stream just before midday on 11 June 1980.

KEY TO THE HONDURAN SPECIES IN THE *E. MILESI* GROUP

1. Toes with lateral fleshy fringes 2
 Toes with well developed lateral keel, but without fleshy fringes (toe IV with weak fleshy fringes in some large female *E. fecundus*) 5
2. Toes extensively webbed, modal formula I 1 1/3 - 2 II 1 1/3 - 2 1/2 III 2 - 3 1/3 IV 3 1/3 - 2 V; males to 41 mm SVL (moderate elevations of central part of Cordillera Nombre de Dios) *E. chrysozetetes*
 Toes moderately webbed, modal formula I 2 - 2 3/4 II 2 - 3 1/2 III 3 - 4 IV 4 - 2 1/2 V or I 2 - 2 3/4 II 2 - 3 1/2 III 3 - 4 1/4 IV 4 1/4 - 2 3/4 V; males less than 34 mm SVL 3
3. Toes III-IV or only toe IV (some males) with lateral fleshy fringes; webbing on toes III-V slightly reduced, modal formula III 3 - 4 1/4 IV 4 1/4 - 2 3/4 V; males 20.9-26.9 mm SVL (moderate elevations of Sierra de Agalta)... *E. epochthidus*
 Toes II-IV with lateral fleshy fringes; increased webbing on toes III-V, modal formula III 3 - 4 IV 4 - 2 1/2 V; males 27.0-33.2 mm SVL 4
4. Thin, pale middorsal stripe extending from tip of snout to above vent (intermediate elevations of central part of Cordillera Nombre de Dios) *E. cruzi*
 No pale middorsal stripe (moderate and intermediate elevations of western part of Cordillera Nombre de Dios and west-central Yoro to northwestern Olancho) ...
 *E. stadelmani*
5. Upper lip distinctly flared; vocal slits absent in adult males; males 26-30 mm SVL; male tympanum length 72-85 % of eye length (moderate elevations of Sierra de Omoa) *E. omoaensis*
 Upper lip not flared; vocal slits present in adult males; males less than 26 mm SVL; male tympanum length 35-68 % length of eye, or tympanum very indistinct to hidden and unmeasurable 6
6. Modal webbing formula I 2 - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/4 IV 4 1/4 - 2 3/4 V; male tympanic annulus indistinct, very indistinct, or hidden (low and moderate elevations of central and eastern portions of Cordillera Nombre de Dios)
 *E. fecundus*
 Modal webbing formula I - II 2⁺ - 3 4/5 III 3⁺ - 4 1/2 IV 4 1/2 - 3⁺ V or I 2⁺ - 2 4/5 II 2 - 3 3/4 III 3 - 4 1/2 IV 4 1/2 - 3⁺ V; male tympanic annulus distinct or indistinct 7
7. Male tympanic annulus distinct or indistinct, that of female very indistinct; male tympanum length 35-46 % length of eye; occurs in forest well away from streams (intermediate elevations of western and central portions of Cordillera Nombre de Dios) *E. saltuarius*
 Male tympanic annulus distinct, that of female indistinct; male tympanum length 47-68 % length of eye; occurs alongside streams (moderate and intermediate elevations of sierras Omoa and Espiritu Santo) *E. milesi*

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